

Effect of temperature on the growth of the commercially fished common whelk (*Buccinum undatum*, L.): a regional analysis within the Irish Sea

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Fisheries Research

DOI:

[10.1016/j.fishres.2019.105437](https://doi.org/10.1016/j.fishres.2019.105437)

Published: 01/03/2020

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Emmerson, J., Hollyman, P. R., Bloor, I., & Jenkins, S. (2020). Effect of temperature on the growth of the commercially fished common whelk (*Buccinum undatum*, L.): a regional analysis within the Irish Sea. *Fisheries Research*, 223, [105437].
<https://doi.org/10.1016/j.fishres.2019.105437>

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Journal: Fisheries Research

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Effect of temperature on the growth of the commercially fished common whelk (*Buccinum undatum*, L.): a regional analysis within the Irish Sea.

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Keywords: commercial fishery, statolith, age, stock assessment, mollusc, gastropod, conservation

Abstract

In response to increased demand in Asian markets, the commercial fishery for the common whelk (*Buccinum undatum*, L.) has expanded in north-eastern Europe. In the Irish Sea region (ICES Area 20 VIIa), increased effort and landings have raised concerns about long-term stability of the fishery amongst stakeholders. Fisheries in Welsh waters and the Isle of Man territorial sea are now subject to an increased minimum landing size according to the best available scientific data. This study addresses key knowledge gaps by investigating the size-at-age relationship of the species across the latitudinal extent of the fisheries management region. Our findings show that growth parameters, modelled using growth rings observed in the statolith, vary between populations and show a broadly latitudinal pattern. Thermal-time (expressed as sea bottom temperature degree-days) showed a significant negative linear relationship with the asymptotic size reach by whelk populations (L_{∞}), where whelk grew to a larger maximum size in cooler waters. Other parameters, including maximum growth rates and the age at which growth rate begins to decrease, showed clear trends with sea-bottom temperature but linear modelling failed to detect significant relationships, where warmer waters increase the rate of growth in the early life stages of whelk but cooler waters allow growth to continue until later in life. Whilst there are substantial requirements to further validate and refine the relationship between growth and sea-bottom temperature, extrapolation of these data to other regions in Northeast Europe may provide a

valuable tool in approximating important life-history characteristics in stock assessments, such as L_{∞} , age-at- L_{50} and age-at-recruitment.

1.0 Introduction

The common whelk (*Buccinum undatum*, Linnaeus, 1758) is a neo-gastropod mollusc that is found in the subtidal waters of the North Atlantic to depths of 1400 m (Mercier & Hamel, 2008). The species is widely distributed on the Atlantic continental shelf and is frequently found in densities that support commercial fisheries in both Europe and America (Emmerson, et al., 2018; Borsetti, et al., 2018). A small scale fishery has existed in Europe for over a century, with recorded annual landings in England and Wales of 4500 t in 1911 (Dakin, 1912). European waters are the principal area of production (FAO, 2017) and the fishery has undergone significant economic and geographical expansion in response to emerging Asian markets, with global landings increasing from 7000 t yr⁻¹ to over 35000 t yr⁻¹ between 1990 and 2014 (FAO, 2017).

Whelk are the 6th most economically important shellfish species in the UK, with total UK landings (20,800 t) equating to a value of £22.7 million in 2017 (MMO, 2018). What was once a small-scale inshore fishery is now characterised by a fleet increasing in average length and fishing capacity. For UK vessels under 12 m in length, whelk has overtaken crab and lobster as the most important shellfish species by volume caught in the ‘pot and trap’ sector (Lawrence, et al., 2017). For larger vessels (> 12 m) they now rank as the second most important by volume. The same data highlight that over the last decade, the economic significance of whelk has also increased. Among the five most valuable species from 2008 to 2017 in the ‘10-12 m pots & traps’ sector, catch data shows the relative economic contribution of whelk increase by 10%, whereas, European lobster and edible crab value increased merely by 5% and Nephrops decreased by half (SEAFISH Economics, 2018). Regionally, the Irish Sea (ICES Area VIIa) has an estimated 447% increase in the total landed weight of whelk between 2000 and 2016 by British registered vessels, with the most significant increases being recorded in the Isle of Man territorial sea (ICES rectangle 37E5) and Welsh waters (ICES rectangles 33E5, 34E5, 35E5) (Emmerson, et al., 2018). In the Irish Sea, whelk are the third most valuable shellfish resource after *Nephrops* and scallops (*Pecten maximus*), worth £8.5 million in 2017 at first-sale value (16.5% of the

total value of all species landed by UK vessels in ICES VIIa) (MMO, 2018). The value of whelks landed into Wales by UK vessels was greater than all other species combined in 2017 (MMO, 2018).

The sustainability of whelk fisheries has been questioned by both fisheries scientists and industry stakeholders (see Nicholson & Evans, 1997; McIntyre et al., 2015). It is clear, for example, that the widely adopted EU minimum landing size (MLS) (45 mm total shell length; TSL) fails to protect juvenile individuals (individuals below the size of functional maturity; L_{50}) from harvest in many regions of the British Isles (Shelmerdine, et al., 2007; Haig, et al., 2015; Emmerson, et al., 2018). The uncertainty, knowledge gaps and localised variation in basic biological parameters such as maturity (Haig, et al., 2015; McIntyre, et al., 2015), fecundity (Valentinsson, 2002) and mortality (Laptikhovsky, et al., 2016), combined with low resolution data on fishing effort and catch has meant that a conceptual framework for stock assessments has not yet been developed. As a consequence, the fishery is considered ‘data-poor’ and there are no biologically referenced catch or effort restrictions. Fisheries management responses to apparent whelk population declines have therefore been precautionary in approach when compared to management decisions for other commercially important species (Fahy et al., 2000; Fahy et al., 2005; Shrives et al., 2015).

An understanding of size-at-age and longevity of exploited marine species are fundamental in most stock assessment models. For effective fisheries management to take place, scientists must be able to understand changes of stock size and structure in response to dynamic anthropogenic (primarily fishing mortality) and environmental factors (Hilborn & Walters, 1992). Using a size-at-age relationship to estimate parameters such as age-at-recruitment and age-at-first-spawning are especially valuable for evaluating existing management measures that are typically defined using size based metrics, as in the case of whelk fisheries. Modelling the growth parameters of a marine species allows scientists, managers and industry to formulate informed harvesting strategies with a medium-to-long term perspective.

A reliable assessment of age and longevity in whelk populations is problematic for fisheries scientists (Hollyman, et al., 2017b), primarily due to the heterogeneity between populations even over small spatial scales (Shelmerdine, et al., 2007; Haig, et al., 2015). Age determination of this species and other marine gastropods has typically been estimated by counting the growth rings on the operculum,

an organic ‘shield’ on the posterior edge of the animals foot (Santarelli & Gros, 1985). However, issues of precision, accuracy and reliability (see Kideys, 1996) has meant that the methodology is viewed as suboptimal, with < 20% of samples displaying clear readable rings (Hollyman, 2017a). Novel techniques examining the statolith, which are an accretory calcareous particle typically < 300 μm and integral to the animals central nervous system, have been developed to assess age and growth of gastropod molluscs (Barroso, et al., 2005; Chatzinikolaou & Richardson, 2007). This has led to a significantly improved degree of accuracy, precision and reliability in determining the age and growth parameters of whelk (Hollyman, et al., 2018). Observing annual periodicity of growth rings in the statoliths of whelk has also been validated using controlled laboratory tank-rearing experiments (Hollyman, et al., 2018a) and by direct chemical analysis of the calcium carbonate structures themselves (Hollyman, et al., 2017b).

Body temperature (T_b) affects the behaviour and physiology of ectotherms (Huey & Stevenson, 1979; Angilletta Jr., et al., 2002), including aspects such as locomotion (Bennett, 1980; Young, et al., 2006), sensory input (Werner, 1976), and rates of feeding and growth (Navaro & Iglesias, 1995). Hollyman (2017a) observed clear variation in growth rates and seasonality of growth in whelk across the British Isles. Across this latitudinal range, warmer sea bottom temperatures in the south stunted L_∞ (the theoretical average maximum size of the sampled population) and whelk in cooler waters to the north were hypothesised to have a greater time-window within which shell growth could occur, maximising L_∞ values. Variable growth rates were highlighted by Haig et al. (2015) as a potential key driver in localised variation in size-at-maturity (L_{50}) and size-structure of whelk populations sampled in South Wales. Haig et al. (2015) also hypothesised that these observations were likely a consequence of local temperature regimes. Whelk experience a large range of sea temperatures across the geographical range of the species (0 – 22 $^{\circ}\text{C}$; Smith, et al., 2013). Physiological processes are bound by critical thermal limits, beyond which the processes cease, defined as the critical minimum (CT_{min}) and critical maximum (CT_{max}) T_b that permit performance (Angilletta Jr., et al., 2002). The thermal performance curve of whelk is not known but typically may be asymmetric with maximum performance of individuals occurring at some intermediate temperatures (Angilletta Jr., et al., 2002), otherwise known as a *thermal preferendum* (Sharpe & DeMichele, 1977).

Degree-days are an increasingly popular method for explaining variation in growth and development of marine organisms (Chezik, et al., 2014), despite only accounting for 5% of all temperature related growth studies between 1980 and 2006 (Neuheimer & Taggart, 2007). Neuheimer and Taggart (2007) found strong linear functions of the DD metric can explain > 92% of the variation in size-at-age data among forty-one data sets representing species from a variety of marine and freshwater environments as well as laboratory studies. Since the metabolic functioning of whelk, a boreal species, is expected to decrease linearly from a *thermal preferendum*, we model temperature as a function of DD (Sharpe & DeMichele, 1977; Angilletta Jr., et al., 2002).

This study presents a regional analysis of data from statolith samples collected in the Irish Sea, specifically from within Welsh waters and the Isle of Man territorial sea. Spatial comparisons of the size-at-age relationships are coupled with satellite-derived sea-bottom temperature data in an attempt to empirically explain the relationship between temperature and growth parameters for this geographical area.

2.0 Materials and methods

2.1 Biological samples

Whelk were collected by industry participants from exploited fishing grounds in both the Isle of Man territorial sea and Welsh waters (Figure 1) using industry-standard Fish-tec[®] pots (see Emmerson et al., 2018 for details). Samples were collected in the Isle of Man during autumn 2016, whilst samples in Wales were collected through 2016 to spring 2017. The whelks were not ‘graded’ according to MLS to ensure that the maximum range of size classes were available for analysis. They were stored in freezers at -20°C upon landing. Precise spatial details of the sampling locations are not presented in agreement with the participants’ requests to protect commercially sensitive data. After thawing, the TSL of each whelk was measured to the nearest 0.1 mm using Vernier callipers.

<Figure 1>

Figure 1. A map of the Irish Sea showing the general locations where whelk (*Buccinum undatum*) were sampled. A = Isle of Man, B = Amwlch, C = Nefyn, D = Bardsey Island, E = Carmarthen Bay and F = Swansea Bay.

2.2 Statolith analysis

One statolith from each specimen was extracted using the methodology described by Hollyman, et al. (2018a). The statoliths were mounted onto separate microscope slides using CrystalbondTM 509 thermoplastic resin and imaged under a Meiji Techno MT8100 microscope with a Lumenera Infinity 3 microscope camera at 20x magnification. Extracted statoliths were visually assessed according to the rankings described by Hollyman et al. (2018) (see figure 3 in Hollyman et al. (2018) for a visual comparison of the quality and clarity rankings of statolith rings; StR) and only specimens ranked 3 or 4 were used for subsequent analysis. Photomicrographs were analysed using ImageJ v1.48 (Ferreira & Rasband, 2012) to count and measure the width of each statolith ring (StR) starting with the hatching ring (Figure 2). After initial training by PH, the agreement in age determination by StR between the two readers was 89.2%.

<Figure 2>

Figure 2. An example of a photomicrograph of a statolith (sampled in the Isle of Man territorial sea, June 2016). Red lines indicate the growth rings observed, with the centremost arrow showing the hatching ring. The blue arrow at the extremity of the statolith structure shows the edge of the statolith and is not counted as an annual growth ring.

2.3 Temperature data

Sea bottom temperature (SBT) data for each sampling location were extracted from the Global Ocean Physics Reanalysis Products “GLOBAL-REANALYSIS-PHY-001-030”, which was acquired through the Copernicus Marine Environmental Monitoring Service (CMEMS) (<http://copernicus.eu>).

The data provides global ocean eddy-resolving ($1/12^\circ$ horizontal resolution and 50 vertical levels) reanalysis covering the altimetry era 1993-2016. It is based largely on the current real-time global forecasting CMEMS system. Observations are assimilated by means of a reduced-order Kalman filter. Along track altimeter data (Sea Level Anomaly), satellite Sea Surface Temperature, Sea Ice Concentration and *in situ* temperature and salinity vertical profiles are jointly assimilated. The global ocean output files are displayed on a standard regular grid at $1/12^\circ$ (approximately 8 km), with the most relevant grid square to the sampling location being extracted from the overall time series.

The annual sum of degree-days (with a base temperature, T_0 , near to the minimum temperature in the coldest extremes of the species; *B. undatum*: 0 °C) can be used to explore the relationship between

physiological processes and temperature. Degree-days are an expression of thermal-time (Chezik, et al., 2014) or thermal opportunity for growth (Chezik, et al., 2015), where the degree-day for a single day (DD; °C·days) is expressed as:

$$DD = \frac{(T_{Max} + T_{Min})}{2} - T_0$$

Equation 1.

Data were filtered to include SBT for the period 2010-2016. The time series of daily mean SBT data for each location were then calculated as Annual Degree-Days (°C) (aDD) (equation 2). The number of measurements for each region were equal.

$$aDD = \frac{\sum DD}{time_{years}}$$

Equation 2.

2.4 Modelling growth and L_{∞}

TSL-at-age data of each specimen was calculated using a formula calculated by Hollyman (2017a, p. 183), which estimates y (size TSL; mm) to be a function of x (statolith width; μm) such that:

$$y = 43.439x^{0.4259} (R^2 = 0.96, n = 1719)$$

Equation 3.

The measurements from each ring within each statolith sample were then modelled using equation 3 to create an account of growth for each individual whelk. These data were analysed by location and modelled using equation 4 to estimate the average size at each age (ring) within the sampled populations.

This pre-analytical calculation was necessary to fill data gaps brought about by difficulties in sampling small whelks under the 45 mm MLS, so that growth curves could be modelled with a greater goodness-of-fit to size-at-age data. Importantly, this technique avoided the unrealistic application of $TSL \leq 0$ mm at age t_0 (hatching), which would result in incorrect asymptotic estimates (Hollyman, et al., 2018).

Using R (R Core Team, 2017), the size and age data for each observation were modelled using a non-linear least squares regression model fitted with a gompertz growth curve (Tjörve & Tjörve, 2017),

which captures the sigmoidal relationship of growth in *Buccinum* and other marine gastropods more than other models (see (Hollyman, 2017a) , whereby:

$$TSL_t = L_{\infty} e^{-e^{-k_G(t-T_i)}}$$

Equation 4.

TSL_t is the size of a whelk shell at time t , L_{∞} is the theoretical average maximum size of the sampled population, k_G is the growth-rate coefficient (which affects the slope), and T_i represents time at inflection of growth (i.e. where the curve is orientated against the x-axis, or when growth begins to slow).

The estimated coefficient value of L_{∞} , k_G and T_i for each sampled population was then plotted against aDD for each location. Further, aDD was also modelled against maturity (L_{50}) estimates taken from existing literature (Haig et al., 2015; Hollyman, *unpublished data*; Emmerson et al., 2018). The relationship between estimated coefficients and aDD were tested using linear regression to assess whether any significant linear relationship exists.

3.0 Results

A total of 1,796 individual statoliths were examined (2,973 ring observations) with a size range from 25.9 mm to 109.4 mm TSL across six locations (figure 3). The oldest whelk sampled had 8 clear growth rings (excluding the hatching ring).

<Figure 3>

Figure 3. Size-frequency histograms of whelk (*Buccinum undatum*) sampled at Amwlch (n=287), Bardesy Island (n = 279), Isle of Man (IOM) (n = 185), Nefyn (n = 278), Saundersfoot (Carmarthen Bay) (n = 278) and Swansea Bay (n = 304).

The pattern of growth of whelks differed significantly by location (figure 4, table 1). L_{∞} ranged between 59.9 mm in Swansea and 116.8 mm in Isle of Man samples. The variation in L_{∞} follows a broadly latitudinal trend, with the larger maximum size of whelk being observed in samples in the northern Irish Sea. In contrast, the growth rate k_G decreased with increasing latitude, meaning that whelks in the south grew at a faster rate (max = 1.04, Carmarthen Bay) than in the north (min = 0.44, Isle of Man).

<Figure 4>

Figure 4. The modelled size-at-age relationship of *Buccinum undatum* by sample site in Welsh waters and the Isle of Man territorial sea. Points represent mean TSL at Age \pm S.E.

<Table 1>

The satellite data show clear seasonal variability in temperature at each location (figure 5). The lowest minimum temperature was in the Isle of Man (5.8 °C) and highest minimum temperature in Carmarthen Bay (6.9 °C). The lowest maximum temperature was also recorded in the Isle of Man (16.5 °C), whilst the highest maximum temperature was in Swansea Bay (18.4 °C) between 2010-2016 (figure 5).

<Figure 5>

Figure 5. The daily sea-bottom-temperature (SBT °C) at each location sampled for whelk in the Irish Sea for the period 2010-2016.

The average aDD for each location varied between 4004 (Isle of Man, coolest) and 4267 (Swansea Bay, warmest). This equates to an average daily difference of 0.72 °C between the warmest and coolest locations.

When the size-at-age parameters are plotted against the average aDD value for each location, there are clear negative trends in the data for all parameters with the exception of k_G which is positive (figure 6). Linear regression analysis shows a significant effect of aDD on L_∞ ($R^2 = 0.72$, p-value = 0.03) and is described by equation 5a. Linear regression was unable to model the effect of aDD on other growth variables to the same statistical certainty, where $p = 0.07$ for K_G and T_i and $p = 0.11$ for L_{50} . Extrapolating the significant linear model of L_∞ over the aDD data available presents a graphical display of the estimated maximum TSL for whelk populations in the Irish Sea (figure 7).

$$\mathbf{5a)} L_\infty = 696 - 0.15 aDD; R^2 = 0.72, p = 0.03 *$$

$$\mathbf{5b)} L_{50} = 317 - 0.06 aDD; R^2 = 0.63, p = 0.11$$

$$\mathbf{5c)} K_G = -5.7 + 0.002 aDD; R^2 = 0.60, p = 0.07$$

$$\mathbf{5d)} T_i = 21.7 - 0.001 aDD; R^2 = 0.59, p = 0.07$$

Equations 5a – 5d.

<Figure 6>

Figure 6. Scatterplots showing the relationship between estimated L_{∞} , Growth rate (k_G), Age at Gompertz inflection (T_i ; years) and functional maturity (L_{50}) of whelk (*Buccinum undatum*) and sea-bottom-temperature (SBT) expressed as annual average degree-days (aDD) in the Irish Sea. The black lines represent the linearly modelled relationships (equation 5a – 5d) while the grey area shows the standard error in the model. Error bars around the point show the standard error in the parameter estimations. N.B no maturity data is available for Carmarthen Bay samples.

<Figure 7>

Figure 7. The aDD~ L_{∞} relationship for whelk, *Buccinum undatum*, extrapolated throughout the data range of average annual sea bottom temperature (2010-2016) for ICES Area VIIa.

4.0 Discussion

Using growth rings observed in statoliths, the size-at-age relationship was modelled for whelk populations in the Isle of Man territorial sea and Welsh waters using specimens harvested by commercial fishers on exploited fishing grounds. The modelled growth parameters varied by location, with a clear latitudinal trend of increasing asymptotic size with latitude in the Irish Sea. The largest potential size (on average) of whelk populations varied from a maximum of 116.8 mm TSL (Isle of Man) in the north to 59.9 mm TSL (Swansea Bay) in the south, a pattern analogous with observations by Hollyman, et al. (2018) where samples were taken across a geographic range from Shetland to Jersey. This pattern is also observed in the size-distribution data for Irish Sea whelk presented in Emmerson et al. (2018). Whilst we observe large variation in size and growth of whelk over latitudinal scales, similar levels of variation have been observed in size-at-maturity and population structure at local levels, suggesting the growth of whelk may vary significantly over local scales (Haig et al., 2015). Studies examining the life history of this species have consistently alluded to or hypothesised that sea-bottom temperature is the fundamental environmental driver of variation (see Bell & Walker, 1998; McIntyre et al., 2015; Hollyman, et al, 2018). This study is the first to test the relationship between growth parameters and SBT using observed data from statoliths sampled throughout the latitudinal extent of a fisheries management area together with SBT derived from modelled satellite data.

A significant negative linear relationship between temperature, expressed as aDD, and L_{∞} was found for the species on a regional scale in the Irish Sea (ICES Area VIIa), where the average maximum size of an individual within a population decreases with increasing average annual sea-bottom temperature. The Swansea Bay area experienced the greatest aDD of 4267 between 2010 and 2015 with populations showing L_{∞} of 59.9 mm TSL. Cooler waters in North Wales around the Llyn peninsula (aDD = 4174) and Anglesey (aDD = 4017) meant whelk there reached a larger L_{∞} , 89.6 mm and 90.9 mm TSL respectively. The coolest waters were in the Northern Irish Sea around the Isle of Man (aDD = 4004) where whelk grow to the greatest maximum size observed in this study (L_{∞} = 116.8 mm TSL). The variation in estimated size-at-age produced by the gompertz model (figure 4) was larger in the Isle of Man sample than in other samples. Intra-site analysis showed that this increased variation resulted from cross-sampling across several distinct whelk populations on the east coast of the Isle of Man, with ‘Northeast’ and ‘East’ sites exhibiting significantly different size structures (see Emmerson, et al., 2018). Low sample size for each site prevented separate analysis of statoliths, highlighting the need for spatially specific sampling at local scales, particularly where localised hydrographic and bathymetric variations affect ambient temperature. Significant differences in growth rate between the northeast area of the Isle of Man and the rest of the territorial sea have also been observed in king scallop populations (Dignan, et al., 2014).

Other Gompertz growth coefficients (K_G and T_i), i.e. the maximum rate of growth and the point of growth rate inflection, showed marginally non-significant linear relationships with aDD ($p = 0.07$ for both coefficients). Increased sampling may change the outcome of these analyses, since visual interpretation of the data (figure 6) shows that there is a trend between aDD and both K_G and T_i . The maximum rate of growth (K_G) showed a strong positive correlative trend with aDD, where populations of whelk in Swansea Bay and Carmarthen Bay (South Wales) had the highest coefficient value, 0.98 and 1.04 respectively. These values indicate that the warmer sea bottom temperature, whilst limiting the maximum potential size of whelk, also accelerates the rate of growth of individual during early life-stages. The slowest growth-rate coefficient value was observed in cooler waters around the Isle of Man ($K_G = 0.44$). The point at which this gompertz growth rate begins to decrease from the maximum (T_i) showed a negative correlative trend with aDD. Growth of whelks in warm waters such as Swansea Bay

begins to decrease at age 0.94 years, whereas in the Isle of Man growth rate begins to decrease at 2.81 years.

Whelk populations found at higher latitudes in the northern hemisphere generally have a larger maximum body size than those living further south (Hollyman, 2017a), despite initial slower growth rates. This is a common pattern among many ectotherms, such as the scallop *Pecten maximus* (Chauvaud, et al., 2012). Chauvaud et al. (2012) observed that low annual growth rates in northern populations are not due to low daily growth rates, but rather a fewer number of days (thermal window) within which scallop growth could occur, which was also hypothesised in the case of whelk by Hollyman (2017a). Chauvaud et al. (2012) also showed that, “despite initial lower annual growth performance ... differences in asymptotic size (L_{∞}) as a function of latitude resulted from persistent annual growth performances in the north and sharp declines in the south”. Classical growth models have failed to capture this dynamic in long-lived ectotherms that have thermally constrained growing seasons (Chauvaud, et al., 2012), such as whelk. The growth observed in the data for whelk in the Irish Sea point to Bergmans rule, “a general trend of animal sizes to increase with latitude” (Blackburn, et al., 1999). Clearly, higher ambient temperature drives rapid growth in whelk in the early life-stages of the species with larger time-windows for growth, but they reach a smaller asymptotic maximum size earlier in life. These patterns are captured in the behaviour of the gompertz curve, which explained growth in *Buccinum* with a greater R^2 and goodness-of-fit values than other analyses (Hollyman, et al., 2018). We also hypothesise that as well as being temperature drive, the time-window for growth decreases with age in whelks, which is consistent with the notion that as they mature there is a trade-off between growth and reproduction or defence, resulting in a decrease in the length of growing season with age (Stearns, 1992; Lankford, et al., 2001). Chauvaud et al. (2012) were able to demonstrate with scallops that the decrease in the length of growing seasons with age is more rapid at lower latitudes, a hypothesis that may also be reflected in the data presented here.

It is important that data and models explaining species life-history are incorporated into fisheries management where possible. Whelk fisheries in both the Isle of Man and Wales are considered “data poor” though they are managed primarily with an MLS informed by size-at-maturity studies (Haig et al., 2015; Emmerson et al., 2018). Viewing the analyses in this study in the context of other work on

whelk in Welsh waters and the Isle of Man (see Haig et al., 2015; Hollyman, 2017a; Emmerson et al., 2018) suggests that, on average, populations reach functional maturity (L_{50}) by age 4. It may therefore be possible to also estimate reproductive characteristics, upon which MLS is ideally referenced, using solely temperature data if the temperature~growth parameters are further investigated and the relationship is substantiated with additional data. Broadly speaking, management of whelk fisheries in the Northeast Atlantic should follow a latitudinal pattern of increasing MLS with latitude. The EU minimum conservation reference size (MCRS) of 45 mm TSL may well be sufficient to protect spawning stock according to L_{50} estimates in parts of the English Channel (McIntyre, et al., 2015), but it is insufficient in the Irish Sea where L_{50} has been shown to be up to 75 mm TSL (Emmerson, et al., 2018). As whelk fisheries continue to expand throughout the British Isles, it is essential that management is both evidence-based and regionalised.

Within the context of the Irish Sea region, a linear relationship sufficiently explains the variation in the SBT- L_{∞} relationship ($p = 0.03$) and provides good cause to suspect the relationship can be explain other growth coefficient factors (K_G and T_i). However temperature in the Irish Sea varies over a relatively narrow range compared to the temperatures experienced by whelk over the full geographical extent of the species. Whelk are highly eurythmic and have been reported to survive in temperatures from below 0 °C to above 22 °C (Smith, et al., 2013). We hypothesize a non-linear relationship between temperature and L_{∞} of this species over its geographical distribution with asymptotic limits to the size of whelk in populations as average SBT approaches the lower and upper critical thermal limits (Figure 8). Indeed, anecdotal evidence supports this hypothesis, such that preliminary observations in the Orkney Islands (northern Scotland) show $TSL_{\infty} \approx 140$ mm at aDD = 3,465 (M. Coleman, *unpublished data*). A broad-range study to explore this relationship would also reveal whether populations of whelk exhibit ecotypic characteristics, where subpopulations may have undergone genotypic adaptations to specific environmental conditions that affect life-history traits such as growth. It is possible that, following successful validation of the DD~growth relationship in further studies by combining both laboratory and field-based methodologies, the growth rate of this species can be modelled throughout its distribution based solely on open source satellite-based temperature data. However, more work is required to validate the relationship in the first instance.

<Figure 8>

Figure 8. A hypothetical illustration of the relationship between degree days ($^{\circ}\text{C}$) and L_{∞} for the common whelk (*Buccinum undatum*).

It is anticipated that refinement of the aDD variable according to critical thermal limits of the species, which are currently unknown, may result in the analytical models showing a statistical significance in the temperature \sim growth relationship for all parameters. This study analysed the growth parameters of whelk against a single aDD value (the average annual DD for the period 2010-2016), however further investigations looking into the parameters that define DD over time (the maximum rate of increase in DD (DDr), the point of inflection in DD (DDi) during the year) are warranted. That is to say, the mechanistic effect of temperature on whelk may be such that aDD, which calculates the average annual thermal input into the environment, has limited explanatory power. Instead, for example, it may be that it is the *rate* of thermal input within specific season that provides greater statistical power in explaining growth. In order to precisely analyse these hypotheses and to observe localised hydrographic anomalies, temperature data would have to be generated from direct observations using temperature loggers fixed to the seabed as opposed to the low resolution satellite data used in this study. Another method that may further validate the temperature \sim growth relationship would be laboratory-based studies, which control the temperature of the environment as a fixed variable in order to fully understand the specific thresholds that drive and limit the energetic input into shell growth, as well as the species specific *thermal preferendum*. In contrast to this study, which conducted a post-hoc analysis using available temperature data, controlling for temperature as part of the experimental design would add greater certainty to the relationship. The importance of understanding the environmental context of sampling locations (fishing grounds) has been highlighted previously (Hollyman, et al., 2018). Indeed, any specific *thermal preferendum* that exists to encourage energetic investment in shell growth for this species would necessitate an experimental design that controlled for specific thermal parameters as well as other confounding variables (e.g. food availability (Nasution & Roberts, 2004), predatory pressure and aquatic chemistry). Given the opportunistic post-hoc nature of this study, and that the analysis was performed on aggregated one-dimensional temperature data (aDD), it is encouraging that a clear and significant relationship is observed (figure 7).

This study presents the first comparison of growth rates of sampled whelk populations throughout the latitudinal extent of a fisheries management region (ICES VIIa), using data modelled from statolith analysis. A linear trend was observed between SBT, expressed as aDD , and L_{∞} whereby warmer waters limited maximum shell size. When extrapolated throughout the entire geographical extent of ICES VIIa, the data broadly mirrors the reported parameters in other studies. Further verification of the temperature ~ growth relationship for this species is required, combining both broad geographical collaborations and controlled laboratory methodologies. Validating this relationship may lead to broad-scale extrapolations throughout the species distribution, which would provide an incredibly valuable and timely resource to fisheries managers who would otherwise depend on dedicated sampling studies to understand the life-history parameters of whelk stocks, which are currently recognised as being data-poor and potentially over exploited.

Acknowledgments

This project would not have been possible without the help of the Welsh Fisherman's Association (WFA), the Manx Fish Producers Organisation (MFPO) and other members of the fishing industry that voluntarily provided biological samples. The project was funded in Wales by the Welsh Government and in the Isle of Man by the Isle of Man Government's Department for Environment, Food & Agriculture (DEFA). We would also like to extend our gratitude to all those who responsible for directing and overseeing projects associated with this research, including Michel Kaiser, Chris Richardson and Charlotte Colvin. We would also like to thank Claire Lambden for assistance in extracting statoliths from samples.

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Table 1. Summary of results from growth models for each location, including parameter estimates for model coefficients, where L_{∞} is estimated maximum shell size, k_G is the growth-rate coefficient and T_i is the point of inflection in the model curve. Parameter statistical significance shown by p-value (***) = <0.001).

| Model | Param | Est | S.E | t-value | sig. |
|----------------|--------------|-------|------|---------|------|
| Isle of Man | L_{∞} | 116.8 | 4.77 | 24.5 | *** |
| | k_G | 0.44 | 0.02 | 17.7 | *** |
| | T_i | 2.81 | 0.11 | 24.5 | *** |
| Anglesey | L_{∞} | 90.9 | 1.45 | 1.162.6 | *** |
| | k_G | 0.72 | 0.03 | 22.2 | *** |
| | T_i | 1.47 | 0.03 | 44.2 | *** |
| Nefyn | L_{∞} | 89.6 | 1.19 | 74.9 | *** |
| | k_G | 0.71 | 0.03 | 24.2 | *** |
| | T_i | 1.59 | 0.03 | 55.9 | *** |
| Bardsey | L_{∞} | 91.5 | 0.99 | 92.0 | *** |
| | k_G | 0.74 | 0.03 | 26.2 | *** |
| | T_i | 1.96 | 0.04 | 54.6 | *** |
| Carmarthen Bay | L_{∞} | 81.9 | 1.49 | 54.9 | *** |
| | k_G | 1.04 | 0.06 | 16.8 | *** |
| | T_i | 1.14 | 0.04 | 30.3 | *** |
| Swansea | L_{∞} | 59.9 | 1.77 | 33.7 | *** |
| | k_G | 0.98 | 0.06 | 11.1 | *** |
| | T_i | 0.94 | 0.08 | 13.5 | *** |

Figure 1
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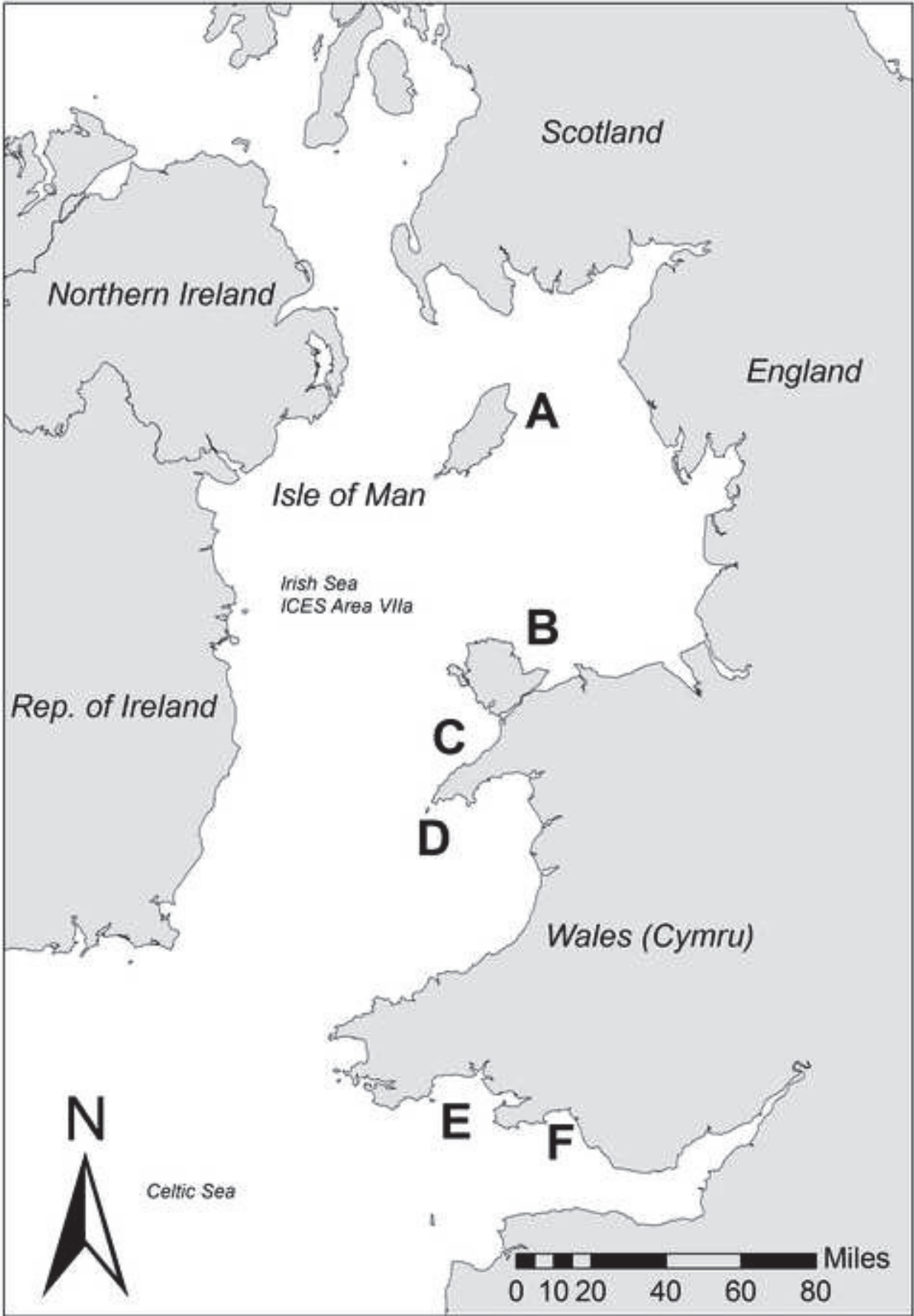


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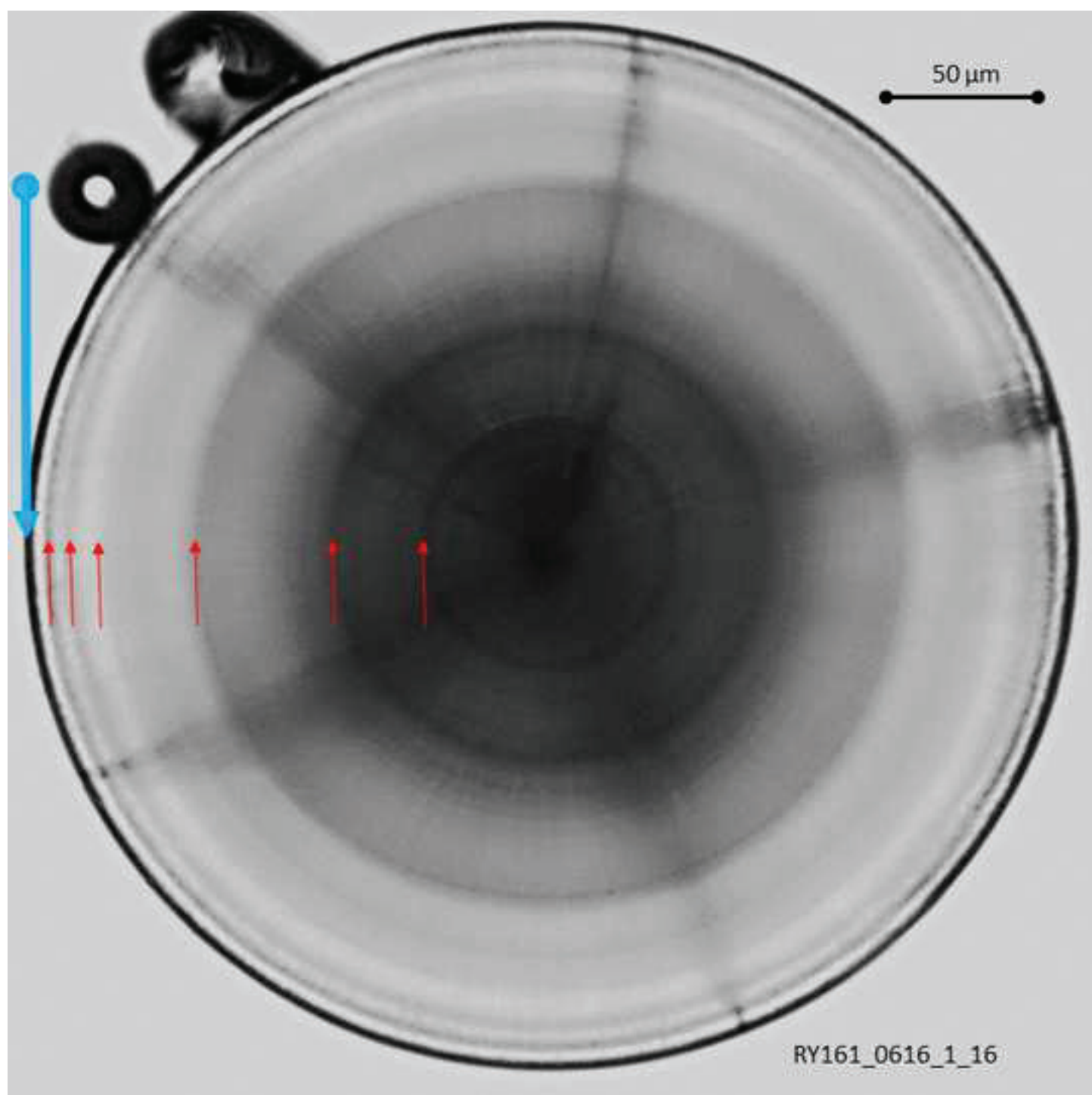


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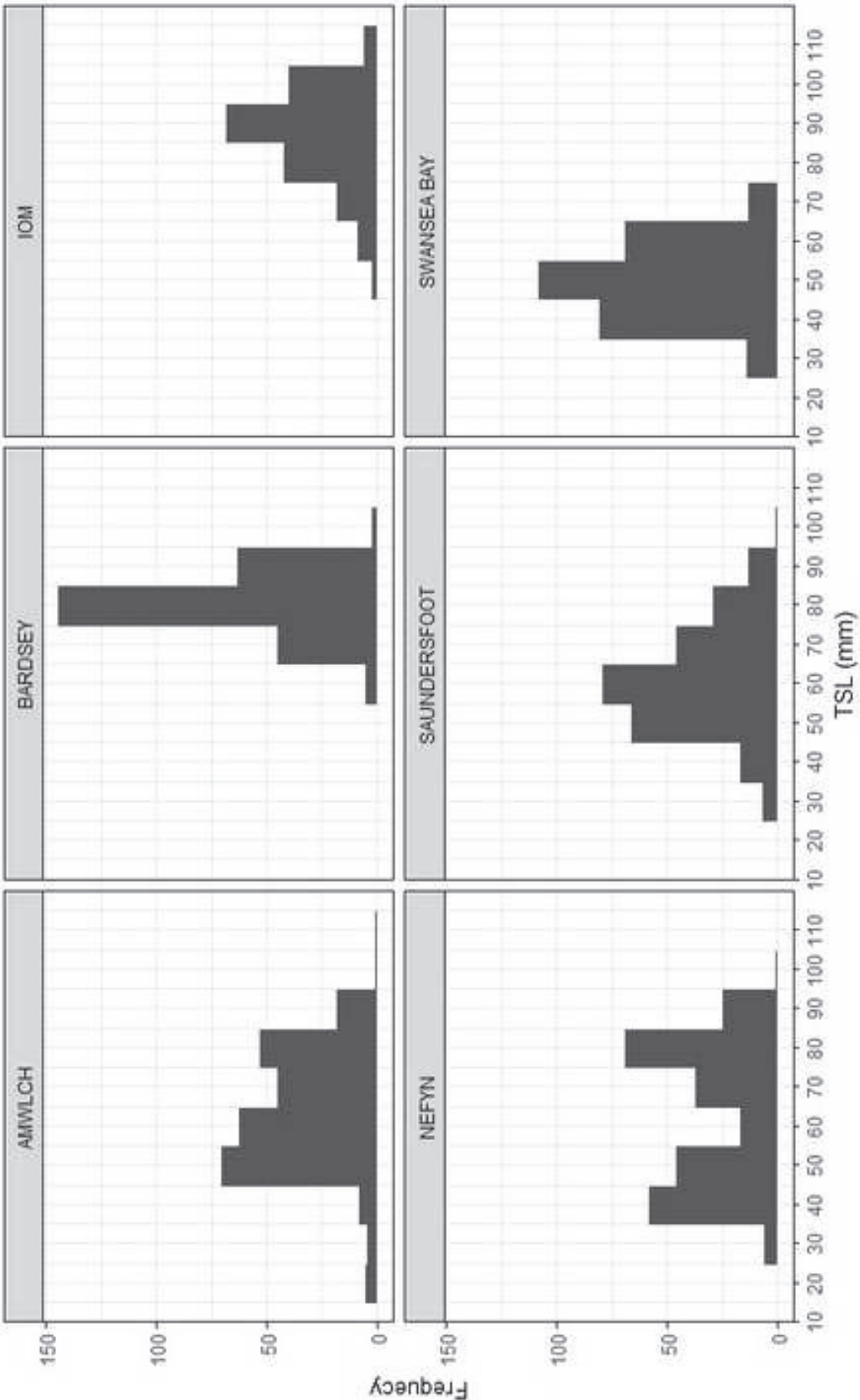


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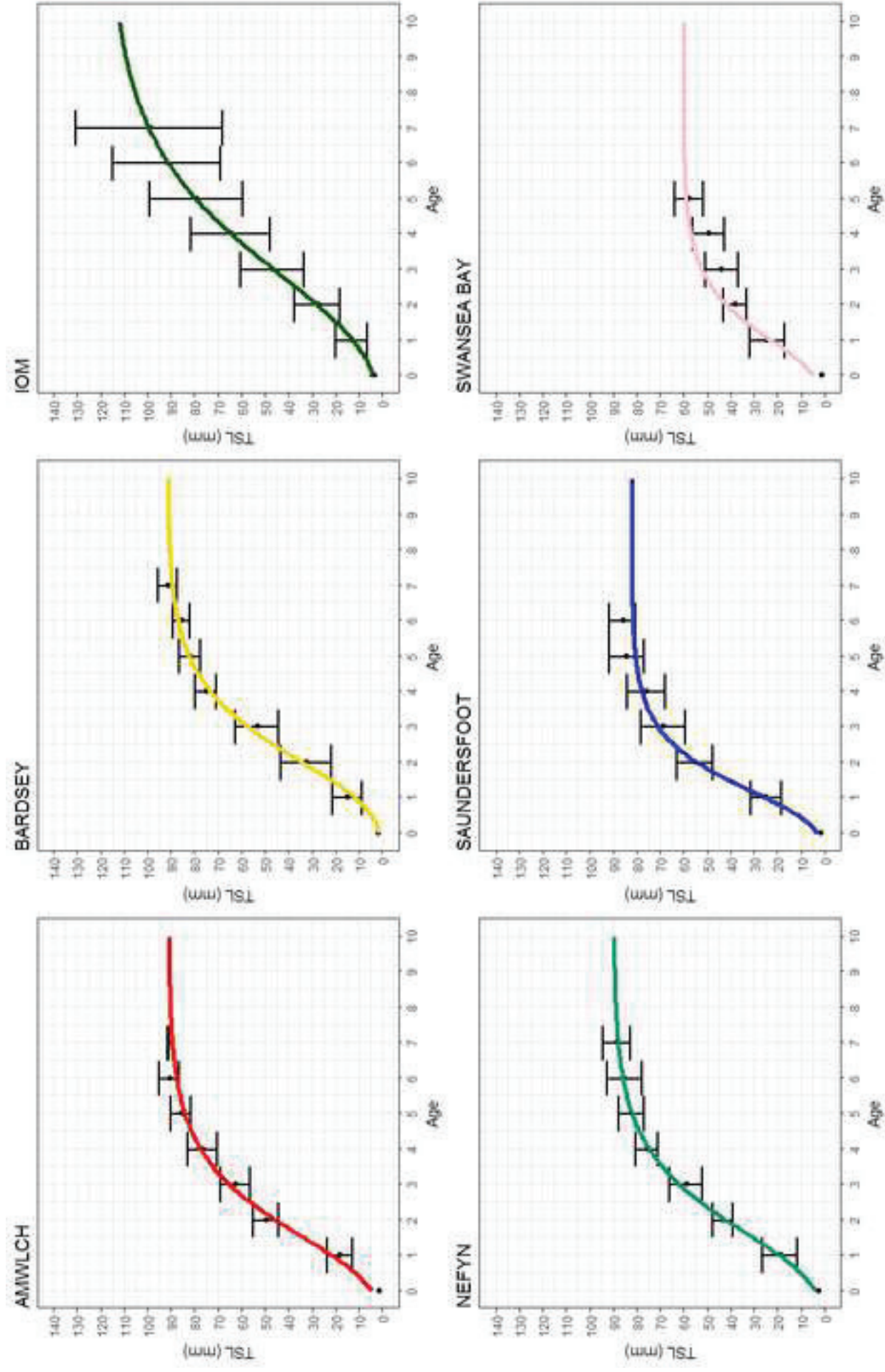


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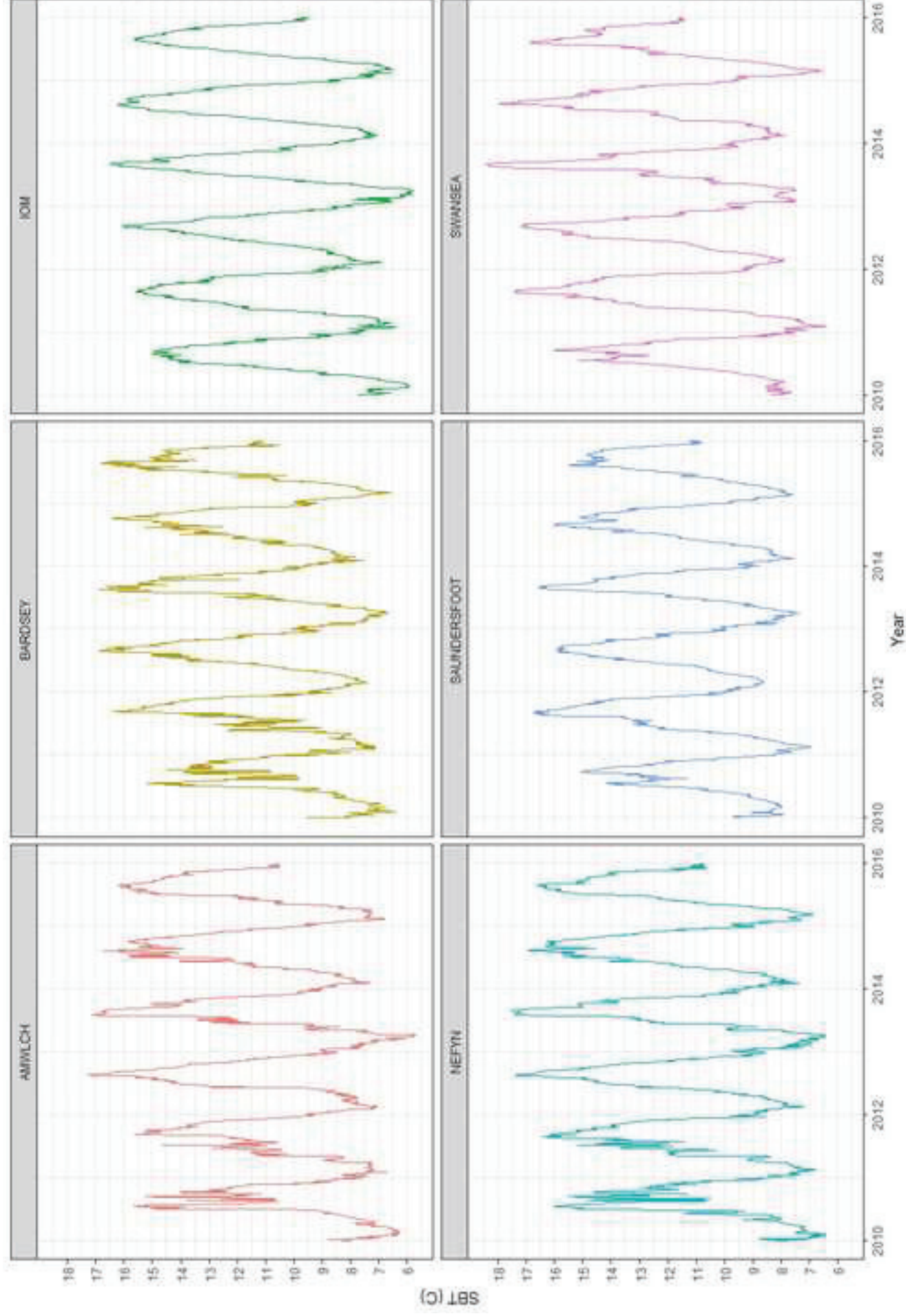


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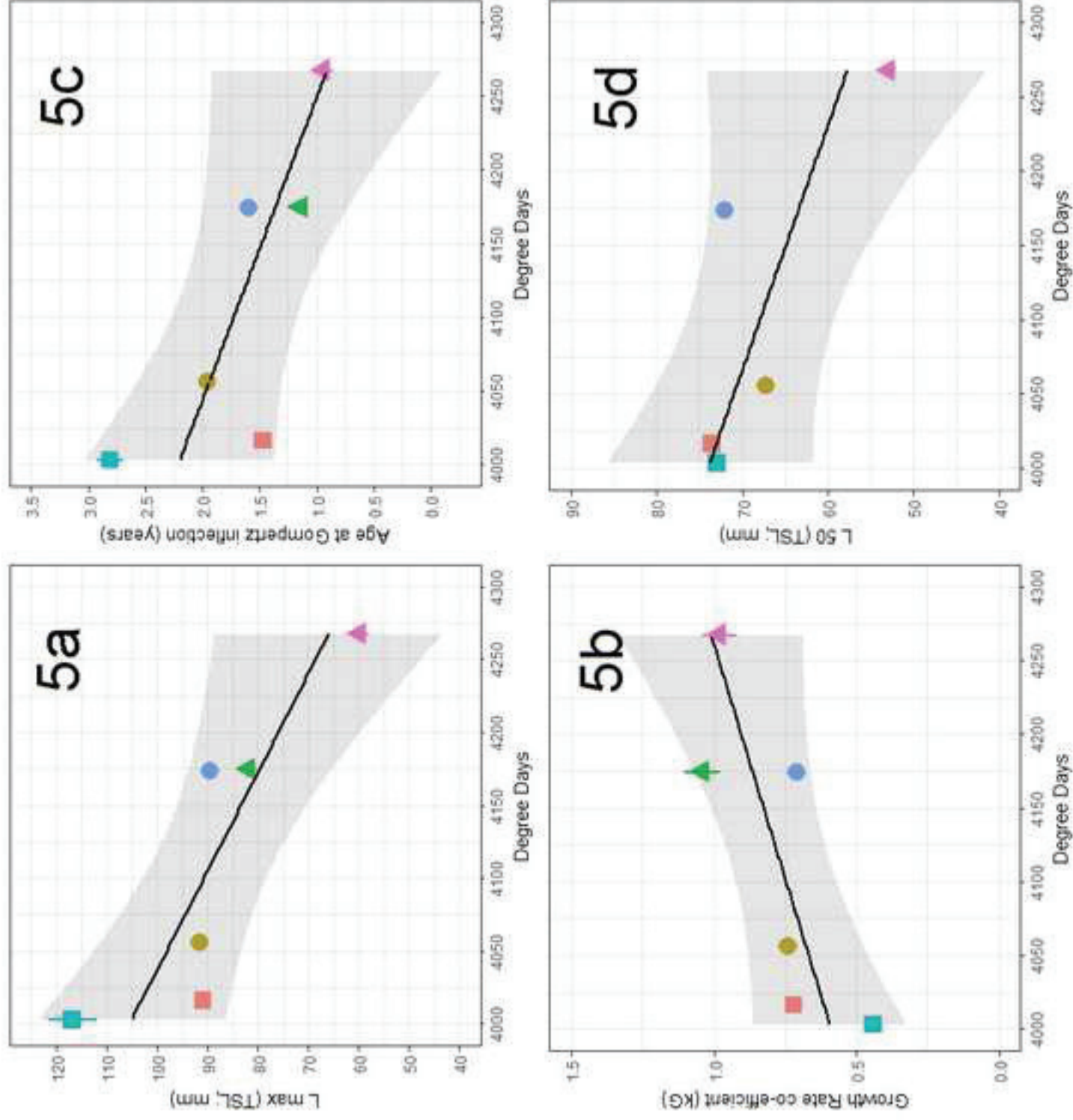


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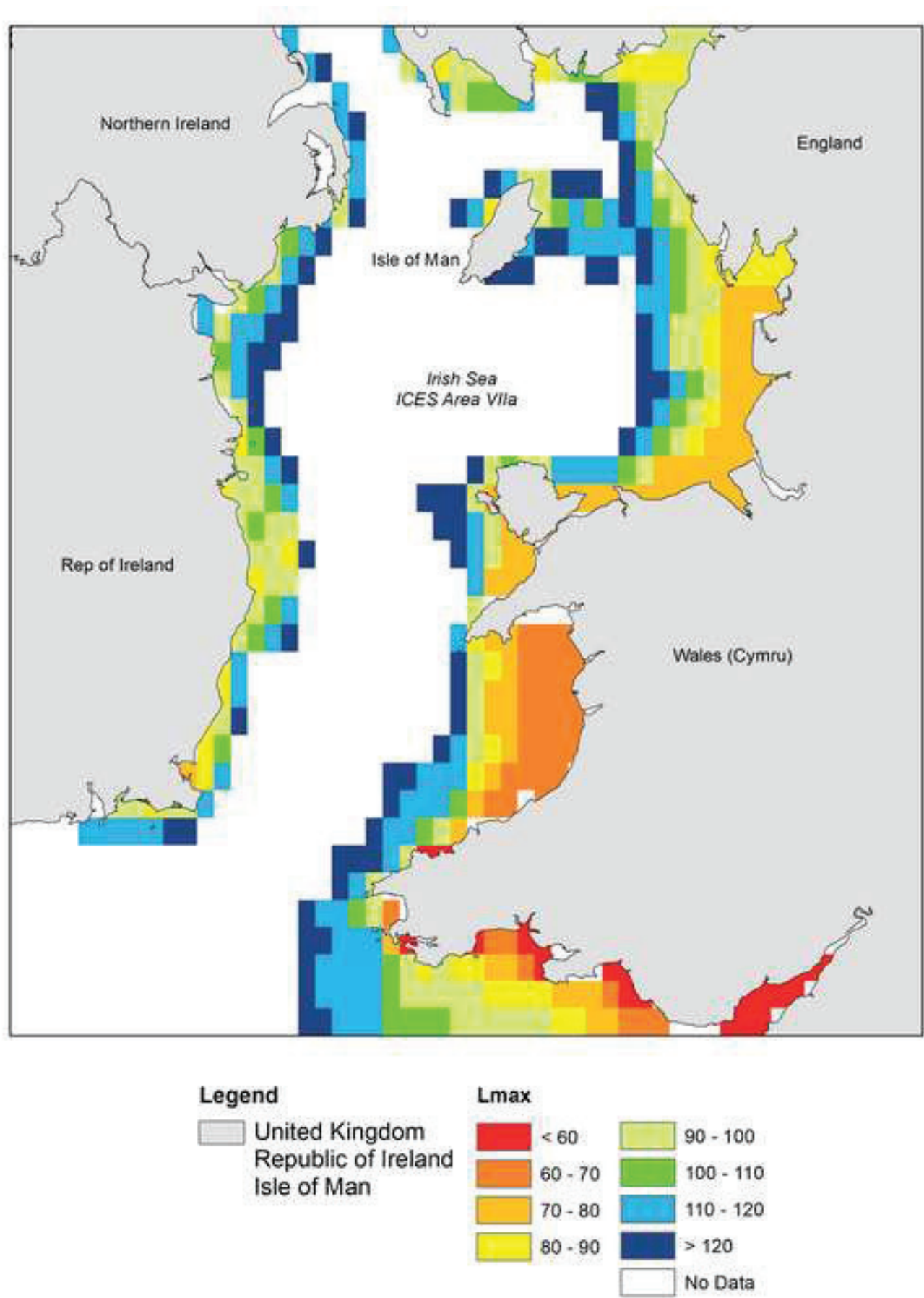


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